

## NEKTON USE OF DIFFERENT HABITAT TYPES IN SEAGRASS BEDS OF LOWER LAGUNA MADRE, TEXAS

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### ABSTRACT

We compared densities of fishes and decapods among three types of undisturbed seagrass beds (*Halodule wrightii*, *Syringodium filiforme*, and *Thalassia testudinum*) and three dredged material areas (old deposits revegetated by mixed seagrasses, and new experimental deposits planted with *Halodule wrightii* or left to revegetate naturally). Planted beds failed, and both types of experimental deposits remained nonvegetated sandy mud throughout the study. We collected nekton with a 1-m<sup>2</sup> enclosure sampler in spring and fall of both 1996 and 1997, simultaneously collecting data on seagrass, sediment, and water column characteristics. Densities of total fishes, total decapods, and most numerical dominants were usually significantly higher in seagrass beds compared with nonvegetated bottom, as were fish and decapod biomasses. Among seagrass beds, nekton densities were often significantly higher in revegetated dredged material and *Thalassia testudinum*, particularly in spring. Regression models indicated that densities of most dominant species were related primarily to seagrass characteristics and less to sediment or water column parameters. Nekton densities in Lower Laguna Madre seagrass beds were typically lower than those found elsewhere in the Gulf of Mexico, but the large acreage of seagrasses in this estuary probably supports the high fisheries productivity found along the south Texas coast.

The Lower Laguna Madre (LLM) of Texas is a euhaline estuary that supports extensive beds of seagrasses that are considered important habitat for many fishery and forage species (Hoese and Jones, 1963; Bell and Pollard, 1989; Minello, 1999). Plant species present in the seagrass beds vary spatially but are primarily shoalgrass *Halodule wrightii*, manatee grass *Syringodium filiforme*, and turtle grass *Thalassia testudinum* and secondarily clover grass *Halophila engelmannii* and widgeon grass *Ruppia maritima*. Seagrass meadows are typically dominated by one species determined by water clarity, depth, and salinity (Onuf, 1996). A variety of studies have documented higher densities of nekton in seagrasses than in adjoining nonvegetated habitats (for example, see recent studies by Connolly, 1994; Edgar and Shaw, 1995; Sheridan et al., 1997; Arrivillaga and Baltz, 1999; and earlier references cited therein), although this pattern can vary (Jenkins et al., 1997). However, less is known about the relative value and use of different seagrass species for nekton. Some studies report differences in nekton densities in different but adjoining species of seagrasses (Stoner, 1983; Rooker and Holt, 1997), others do not (Worthington et al., 1992; Zupo and Nelson, 1999), and still others show mixed results (Kenyon et al., 1995; Sheridan et al., 1997; Loneragan et al., 1998). Seagrasses generally are considered to supply food and protection to juvenile fishes and decapods, and the capacity for providing these services may vary among the seagrass species (Lewis, 1984; Kenyon et al., 1995).

In addition to extensive seagrass beds, another dominant characteristic of Lower Laguna Madre is the Gulf Intracoastal Waterway (GIWW). The GIWW was dredged by the U. S. Army Corps of Engineers in the 1940s and bisects the LLM longitudinally, generally on the western side. Periodic deposition of maintenance dredged material into place-

ment areas adjacent to the GIWW has impacted seagrass habitats in the area through direct smothering and possibly through increased turbidity (Onuf, 1994). Deposits of dredged material generally become revegetated with seagrasses under the appropriate conditions, but these newly formed seagrass beds may be functionally different from natural seagrass beds.

The support and impetus for our research project was related to the rate of seagrass revegetation of newly deposited dredged material. We hypothesized that the rate of revegetation could be increased by planting *Halodule wrightii*, a pioneer species, onto dredged material. We expected to compare use of these planted seagrass beds with natural beds and with well-established beds growing on older dredged material. However, the new transplants did not survive, thus the planted areas that we examined were essentially equivalent to nonvegetated sandy mud bottom.

The objective of this study was to compare nekton use of different habitat types within seagrass beds, including naturally revegetated deposits of dredged material and recently deposited, nonvegetated dredged material. The natural seagrass beds we examined were dominated by three different species of seagrass (*Halodule wrightii*, *Syringodium filiforme*, and *Thalassia testudinum*, hereafter referred to by genera only). A quantitative enclosure device was used to sample these different areas and determine density (utilization) patterns.

## METHODS

**GENERAL DESCRIPTION OF THE AREA.** — Laguna Madre is the southernmost estuary of the Texas coast, extending 200 km from Corpus Christi Bay to the Rio Grande delta. Lower Laguna Madre extends from the Land Cut, an area of wind-blown sand that is flooded only on extreme high tides, south about 90 km to Brazos-Santiago Pass near the mouth of the Rio Grande. Seagrasses are generally found in all but the deepest (2–3 m), most turbid waters (Onuf, 1996). Seagrass species composition and temporal changes in coverage in Lower Laguna Madre have been documented by Quammen and Onuf (1993) and Onuf (1996).

Dredged material was deposited on two open bay placement areas beside the GIWW approximately 18 km northwest of Brazos-Santiago Pass (Fig. 1). The north experimental site was in Placement Area 233 (26° 11' 48.3" N, 97° 15' 41.2" W), and the south experimental site was in Placement Area 234 (26° 09' 45.0" N, 97° 14' 46.8" W). These placement areas were 1.5–2.0 m deep before dredging activities took place (Brown and Kraus, 1996). At each placement area, new materials were added to a 60 m × 60 m section located approximately 300 m from the GIWW. Dredging was completed in November 1994. When finished, the deposits resembled flattened cones and the center of each experimental site had an emergent mound of dredged material. Poles extending two meters above the water line were placed at the corners and center of each site.

Sediments at the experimental sites were allowed to consolidate until June 1995. *Halodule* was transplanted from donor beds on the eastern and western margins of Lower Laguna Madre into the southern half of each newly deposited section, making two 60 m × 30 m plots. Planting was conducted in June 1995 (on 1 m centers using plugs of seagrass and sediment in 7.6 cm diameter peat pots) and again in September 1995 (on 0.6 m centers using sediment-free seagrass from 7.6 cm diameter plugs). Water depths were 0.9–1.1 m.

**SAMPLING DESIGN.** — Sampling was designed to test whether the various habitat types examined had comparable sediment characteristics and supported similar seagrass and nekton densities. The six habitat types included experimental deposits of dredged material with and without transplants, older dredged material sites north and south of the experimental sites that were not transplanted but had revegetated (at least 5 yrs post-deposition, but actual age unknown), and undisturbed *Halodule*,

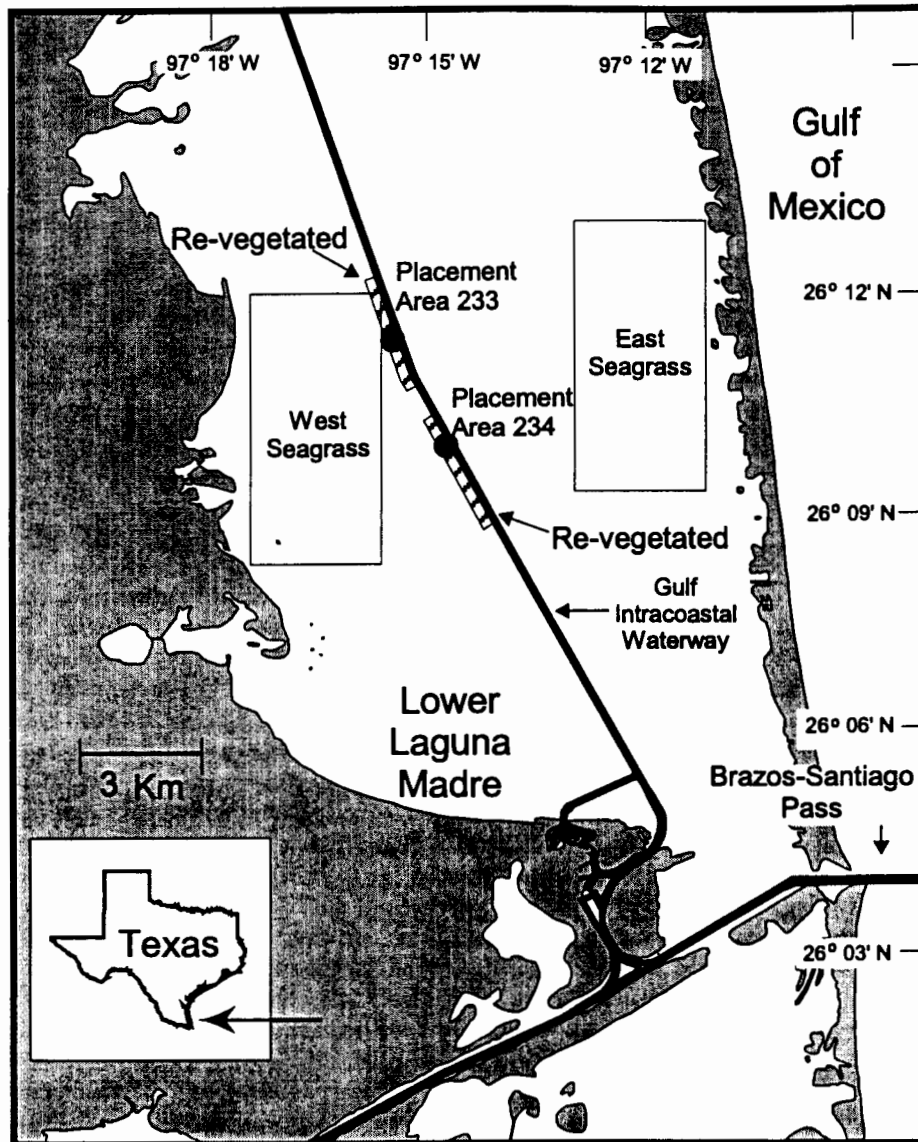


Figure 1. Location of study area in Lower Laguna Madre, Texas. Filled circles (●) indicate positions of experimental dredged material placement sites.

*Syringodium*, and *Thalassia* beds east and west of the experimental sites. Sampling depths were generally standardized to those found at the experimental sites (0.8–1.5 m).

Since there were no a priori quantitative data with which to determine local sampling effort, sample size was derived from a power analysis (Sokal and Rohlf, 1981) of seagrass community measurements along the upper Texas coast (P. Sheridan, unpublished data). With 10–12 samples per habitat type, a 100% difference between two log(x+1)-transformed means could be detected with  $\alpha = 0.05$  and  $1 - \beta = \text{power} = 0.95$  for dominant fauna, seagrass, and sediment variables. Accordingly, a total of 12 replicates per habitat type and 72 samples per period were planned for seagrass and faunal analyses (fewer for sediments, discussed below). Balanced sample sizes were not always achieved. Actual numbers of samples collected are given in Table 1.

Table 1. Sample sizes by habitat type and season for selected measurements during the 1996–1997 study of dredged material deposits (NB = New, bare; NP = new, planted; RE = revegetated by mixed seagrasses) and three types of natural seagrass (HA = *Halodule wrightii*; SY = *Syringodium filiforme*; TH = *Thalassia testudinum*). Nekton includes density and biomass; water includes depth, salinity, temperature, dissolved oxygen, and turbidity; seagrass includes shoot density and biomass.

Parameter	Season	NB	NP	RE	HA	SY	TH
Nekton and water	Spring	24	24	24	24	24	24
	Fall	23	21	24	24	24	24
Seagrass	Spring	24	24	24	24	24	24
	Fall	20	20	22	24	24	24
Sediment $\text{NH}_4^+$	Spring	20	20	17	19	19	20
	Fall	19	18	20	18	20	20
Organic content	Spring 1996	12	12	9	11	11	9
	Fall 1997	12	12	12	12	12	12
Sand content	Spring 1996	12	12	8	10	10	10
	Fall 1997	12	12	12	12	12	12

Sampling was randomized within grids specified for all habitat types. At each experimental site, the two 60 m × 30 m sections (one planted, one bare) were partitioned into eighteen 10 m × 10 m grids, and six grids were sampled from each section. Old revegetated deposits were located at the northern end of Placement Area 233 (near 26° 12' 15.0" N, 97° 16' 0.0" W) and at the southern end of Placement Area 234 (near 26° 09' 0.0" N, 97° 14' 48.0" W; Fig. 1). Because the old revegetated deposits are linear features with sloping sides, sampling was conducted along a 360 m transect divided into 10-m intervals, and six intervals within the appropriate depth range (0.8–1.5 m) were sampled from each old deposit. Seagrass species composition was not controlled in the old revegetated deposits. Undisturbed seagrass beds were located east and west of the experimental sites. The area bounded by 26° 09' 00" – 26° 13' 00" N and 97° 11' 30" – 97° 13' 00" W comprised the East seagrass area, and the area bounded by 26° 08' 00" – 26° 12' 00" N and 97° 16' 00" – 97° 17' 30" W comprised the West seagrass area (Fig. 1). Each seagrass area was divided into 10 s grids of latitude and longitude, and 18 of these grids in each area within the appropriate depth range of 0.8–1.5 m were sampled (six each of *Halodule*, *Syringodium*, and *Thalassia*). Target seagrass species were randomly assigned to each grid, and the center of each grid was located by Global Positioning System (Garmin International, Model 38, Olathe, KA, USA; at the time, position accuracy 100 m). On arrival, the grid was searched for the appropriate seagrass species; if not found, an alternate grid was selected.

Sampling was conducted in April and October 1996 and in April and September 1997. These months were chosen because fish and decapod abundances, in particular, species of recreational and commercial importance, were expected to be relatively high (Simmons, 1957; Hellier, 1962; Hoese and Jones, 1963; Stokes, 1974). September also represents the seasonal peak in aboveground biomass for seagrasses (Pulich, 1985; Dunton, 1990, 1994). All samples were collected during the day. A recent study of fishes and decapods in seagrasses of Florida Bay, Florida, indicated no differences in community composition or density between diurnal and nocturnal sampling (Sheridan et al., 1997).

Fishes and decapods were sampled quantitatively with either drop trap or throw trap techniques, depending upon sediment characteristics and water depth. At all seagrass sites and revegetated deposits, samples were collected with a 1.0 m<sup>2</sup> cylindrical drop trap made of fiberglass with a steel bottom edge that was deployed from the bow of a boat (Zimmerman et al., 1984). The top edge of the drop trap was tall enough (1.7 m) to remain above water, enclosing the entire water column. Average water depth, salinity, temperature, dissolved oxygen, and turbidity were measured within the drop trap before any other activities. Salinity was measured with a temperature-compensated

refractometer and recorded in practical salinity units (psu). Temperature and dissolved oxygen were measured with a YSI Model 55 meter (YSI Inc., Yellow Springs, OH, USA). Water samples for turbidity analysis were collected in screw cap bottles and later tested in the laboratory with an HF Scientific Model DRT100B turbidimeter and a formazin standard (HF Scientific, Ft. Myers, FL, USA). We captured nekton within the drop trap using dip nets and by filtering the water pumped out of the trap through a 1 mm mesh bag. Any organisms visible on the bottom after pumping were removed and added to the mesh bag. At the experimental placement areas, the combination of high tides and soft sediments occasionally forced use of a 1.0-m<sup>2</sup> throw trap (Kushlan, 1981) in lieu of the drop trap. The throw trap was made of 2 mm mesh nylon net with an iron rebar bottom frame and a buoyant PVC plastic top frame and was also tall enough (1.5 m) to enclose the entire water column. The throw trap was deployed off the bow of a boat, then it was retrieved by pushing the leading edge of a 1.4 m<sup>2</sup> bag net (2 mm mesh net on a rebar frame) 5–10 cm into the mud under the throw trap and scooping the entire throw trap up out of the water. The throw trap was removed, sediments were washed out of the bag net, and the contents were collected in a mesh bag. Mesh bags were preserved in 10% buffered formalin-seawater. The use of two different mesh sizes to collect animals potentially increased the number of animals collected by drop trap versus throw trap. These animals would have been between 1–2 mm in any dimension and likely would have been larval or early juvenile stages assigned to family or genus only. The entire data set contained only 110 animals (out of 8731) that were not identified to species (Appendix 1), including 73 *Farfantepenaeus* spp. (see below). Thus we believe the mesh bias was minimal.

In the laboratory, we sorted the samples and identified fauna to species or the lowest feasible taxon. Scientific and common names follow Williams et al. (1989), Robins et al. (1991), and Pérez Farfante and Kensley (1997). Small penaeid shrimps can be difficult to identify. Brown shrimp *Farfantepenaeus aztecus* and pink shrimp *F. duorarum* up to 13 mm in total length (TL) were distinguished by the shape of the antennal scale (Williams 1959); larger specimens were distinguished by characters described primarily by Pérez Farfante (1970) and secondarily by Pearson (1939), Williams (1953, 1959), Ringo and Zamora (1968), Zamora and Trent (1968), Pérez Farfante (1969, 1978), and Pérez Farfante and Kensley (1997). Specimens between 13–18 mm TL could not be reliably identified and, along with damaged shrimp in the genus, were assigned to *Farfantepenaeus* spp.

Sediment pore water NH<sub>4</sub><sup>+</sup> was measured in conjunction with faunal sampling (n = 6–12 for each habitat type each month). Sediment NH<sub>4</sub><sup>+</sup> is generally considered the primary nutrient pool in Laguna Madre (Pulich, 1985; Czerny and Dunton, 1995; Dunton, 1996), and it could be a factor in determining the success and health of seagrass revegetation projects. Sediment samples (top 10 cm) were collected from within the empty drop trap or adjacent to the deployed throw trap in triplicate using a 2.5 cm diameter plastic syringe with the tip removed. Samples were stored in plastic bags on ice during transport and were frozen prior to laboratory analysis. Pore water was extracted by centrifuging thawed sediments and analyzing the supernatant for NH<sub>4</sub><sup>+</sup> following the methods of Parsons et al. (1984). The three replicates were used to estimate means for each site.

Sediment organic content and sand and silt + clay proportions were determined from single syringe samples (collected as above) during April 1996 and September 1997 (n = 8–12 per habitat type each month). Live seagrass roots and rhizomes were removed with forceps from a subsample of sediment that was then dried at 60°C to a constant weight, weighed, combusted at 500°C for 3 h, then reweighed to determine percent organic material lost (modified from Dean, 1974). Rubble (particles >2 mm in any dimension) was removed from another subsample by washing through a 2 mm sieve, then sand and silt+clay proportions were determined following the methods of Folk (1980).

Seagrass coverage, shoot density, and aboveground biomass were measured either within the perimeter of the drop trap or adjacent to the deployed throw trap at each site. Seagrass coverage was estimated by haphazard placement of a single 0.25 m<sup>2</sup> quadrat divided into 100 grids on the bottom, then noting the presence of each species of seagrass within each grid. Shoot density and aboveground biomass were determined by placing three 0.0625 m<sup>2</sup> quadrats on the bottom, count-

ing the number of shoots enclosed, removing all aboveground material, washing sediment from the seagrass, and drying the shoots at 60°C to a constant weight. The three quadrats were used to estimate means for each site.

**DATA ANALYSIS.** — Relationships between faunal densities and habitat type or seagrass, sediment, and water column characteristics were examined by analysis of variance (ANOVA) and linear regression. Using ANOVA, we tested for habitat-related differences in the following nekton groups: total numbers of fishes and decapods; numbers of dominant species (defined as those with counts averaging 1 ind m<sup>-2</sup> in any habitat type in either season during both years); and biomass of fishes, shrimps, and crabs. Comparisons were conducted by season using year as a blocking factor. The main effect of habitat type in the ANOVA consisted of six levels: new dredged material left bare for natural revegetation (NB), new dredged material planted with *Halodule* (NP), old dredged material naturally revegetated by mixed seagrasses (RE), and natural seagrass beds dominated by either *Halodule* (HA), *Syringodium* (SY), or *Thalassia* (TH). Within this main effect, we examined five a priori contrasts to test for specific differences of interest in habitat utilization, including a comparison of nonvegetated and vegetated habitats (NB + NP vs RE+HA+SY+TH), revegetated older dredged material and natural seagrass beds (RE vs HA+SY+TH), and the three combinations of seagrass species within natural beds (HA vs SY, HA vs TH, and SY vs TH).

Examination of the distribution of error terms for abundant macrofauna and for water, sediment, and seagrass characteristics indicated non-normality. However, ANOVA is robust to non-normality particularly if sample sizes are large (treatments  $\geq 5$  and replicates  $\geq 6$ ; Underwood, 1997). Positive relationships between means and variances were detected for all variables, indicating transformation was needed prior to ANOVA. Log(x+1)-transformation was employed for most variables, whereas arcsine transformation was used for percentage data (seagrass species coverage, sediment organic content, sand content). Transformation of nekton and seagrass density and water column characteristics was not always successful in achieving homogeneity of variances prior to ANOVA. Therefore, we conducted analyses using a lower probability level for significance ( $P \leq 0.01$ ; Underwood, 1997). Tabular means are from untransformed data, but ANOVA and multiple comparison results are from transformed data.

We also used simple linear regression to examine relationships between transformed faunal densities and seagrass, sediment, and water column characteristics. Only one variable per seagrass species was permitted in any regression model due to high levels of correlation ( $r = 0.63\text{--}0.88$ ) among variables describing each seagrass species (percent cover, biomass, and shoot density). Forward stepwise regression was used with F-to-enter = 4.00 and F-to-stay = 3.99 in order to control overfitting of equations (Draper and Smith, 1981). Examination of normal probability plots (residuals versus expected normal values) indicated that residuals from final equations were normally distributed. Analyses were conducted using STATISTICA personal computer software (StatSoft Inc., Tulsa, OK, USA, 1995).

## RESULTS

**NEKTON COMMUNITIES.** — We collected 1378 ind among 35 fish taxa and 7353 ind among 29 decapod taxa over the course of the study (Appendix 1). Dominant species included code goby *Gobiosoma robustum*, pinfish *Lagodon rhomboides*, bay anchovy *Anchoa mitchilli* (fall only), bigclaw snapping shrimp *Alpheus heterochaelis*, lesser blue crab *Callinectes similis* (spring only), gulf grassflat crab *Dyspanopeus texana*, brown shrimp *Farfantepenaeus aztecus*, pink shrimp *Farfantepenaeus duorarum*, zostera shrimp *Hippolyte zostericola*, hermit crab *Pagurus criniticornis*, and arrow shrimp *Tozeuma carolinense*. These 11 species constituted 74.0 % of the fishes and 92.3 % of the decapods collected. Several other taxa were relatively abundant ( $\geq 1$  ind m<sup>-2</sup>) during only one or two of the four sampling periods, including longwrist hermit crab *Pagurus longicarpus*

and marsh grass shrimp *Palaemonetes vulgaris* during April 1996, Atlantic mud crab *Panopeus herbstii* during October 1996, brackish grass shrimp *Palaemonetes intermedius* during October 1996 and April 1997, striped anchovy *Anchoa hepsetus* during April 1997, and blue crab *Callinectes sapidus* during September 1997. *Pagurus longicarpus* was found primarily at the experimental dredged material sites, and *Anchoa hepsetus* was collected there and over *Thalassia*. *Callinectes sapidus*, *Palaemonetes intermedius*, *Palaemonetes vulgaris*, and *Panopeus herbstii* were collected in one or more seagrass habitats.

We found significant differences among habitat types in densities of total fishes, total decapods, most dominant taxa, and total number of nekton species during both spring and fall (Table 2). Seasonal density differences were broadly associated with comparisons of vegetated versus nonvegetated habitats (Table 3) that, for the most part, indicated significantly higher densities and greater numbers of species in vegetated habitats. Only two species, *Anchoa mitchilli* and *Pagurus criniticornis*, were significantly more numerous in the nonvegetated newly-dredged habitats than in any type of seagrass bed, and this was only during the fall.

There were differences in nekton densities among types of seagrass beds, more so in the spring than in the fall and more so among decapods than fishes (Table 3, Fig. 2). Among natural seagrass habitat types, fish densities and biomass were significantly higher in *Thalassia* beds but only during spring. Fall fish densities were relatively uniform over vegetated habitats, with occasional significantly higher densities in *Syringodium* than in *Halodule*. In general, fish densities were somewhat higher during fall than spring seasons. During spring, densities of *Callinectes similis*, *Dyspanopeus texana*, crab and shrimp biomasses, and the total number of nekton species were significantly higher in revegetated dredged material deposits than in natural seagrasses (Table 3, Fig. 2). There were some habitat-specific differences in decapod densities during the fall, but consistently higher densities were only found for *Alpheus heterochaelis* in *Thalassia* and for *Tozeuma carolinense* in *Halodule*.

There was considerable variation in nekton species densities among years and seasons. Neither of the two regularly abundant fishes, *Gobiosoma robustum* and *Lagodon rhomboides*, demonstrated consistently higher densities in one habitat type over another, except for comparisons of vegetated and nonvegetated substrates (Fig. 3). Seasonal densities were similar between years, with a few notable exceptions. Fall densities of *Gobiosoma robustum* in *Syringodium* were much higher during 1997 than 1996 (8.3 fish  $m^{-2}$  versus 2.3 fish  $m^{-2}$ ). Spring densities of *Lagodon rhomboides* were higher in revegetated dredged material deposits and in *Thalassia* in 1996 (3.2 fish  $m^{-2}$  and 3.9 fish  $m^{-2}$ ) than in 1997 (0.1 fish  $m^{-2}$  and 2.3 fish  $m^{-2}$ ).

Two of the dominant shrimps were the economically important *Farfantepenaeus aztecus* and *F. duorarum*, both of which make shallow daily burrows. While selecting vegetated habitats, neither species appeared to select a particular seagrass type (Tables 2,3). In addition, these species exhibited contrasting seasonal and annual patterns: *F. aztecus* was more numerous during spring, particularly Spring 1997, while *F. duorarum* was more numerous during fall (Fig. 4).

Two other dominant shrimps were seagrass canopy residents. *Hippolyte zostericola* was distributed across all seagrass habitat types, but densities in spring were significantly higher in *Thalassia* than in *Halodule* or *Syringodium* (Fig. 5). These differences were associated with higher densities in *Thalassia* during 1997 than 1996. *Tozeuma carolinense*



Table 2. Mean density (number  $m^{-2}$  and standard error, SE) and biomass (g wet weight) of dominant nekton taxa and total number of species in three types of dredged material deposits and three types of natural seagrass beds in Lower Laguna Madre, Texas, during spring (April 1996 and 1997) and fall (October 1996 and September 1997) seasons. P values for the ANOVA main effect of Habitat are given.

	Dredged material deposits						Seagrass beds						P
	New, bare		New, planted		Revegetated		Halodule		Syringodium		Thalassia		
	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	
Spring													
Fishes	1.8	0.3	1.8	0.4	4.4	0.6	2.5	0.6	3.9	0.9	6.7	0.7	<0.001
Gobiosoma robustum	0.0	0.0	0.0	0.0	0.4	0.1	0.3	0.1	0.7	0.3	1.4	0.3	<0.001
Lagodon rhomboides	0.0	0.0	0.0	0.0	1.6	0.6	1.4	0.5	1.6	0.5	3.1	0.6	<0.001
Fish biomass	0.8	0.3	0.8	0.3	13.9	11.5	1.3	0.3	1.4	0.3	4.2	1.4	<0.001
Decapods	6.0	1.9	10.8	3.5	30.5	4.5	12.9	1.5	18.0	3.3	21.5	3.2	<0.001
Alpheus heterochaelis	0.2	0.2	0.1	0.1	1.3	0.4	0.1	0.1	0.5	0.2	2.0	0.6	<0.001
Callinectes similis	0.7	0.2	0.4	0.1	2.5	0.4	1.5	0.4	0.3	0.2	0.1	0.1	<0.001
Dyspanopeus texana	0.1	0.1	0.0	0.0	6.0	1.7	0.8	0.2	1.9	0.5	2.6	0.4	<0.001
Farfantepenaeus aztecus	0.7	0.3	0.5	0.1	3.8	0.9	4.0	0.7	3.5	0.8	1.1	0.3	<0.001
Farfantepenaeus duorarum	0.1	0.1	0.1	0.1	2.5	0.5	1.2	0.3	1.3	0.3	1.7	0.3	<0.001
Hippolyte zostericola	0.5	0.5	0.2	0.1	7.2	1.6	2.6	0.6	4.7	1.5	8.9	1.6	<0.001
Pagurus criniticornis	0.7	0.5	5.4	3.3	1.1	0.5	0.1	0.1	0.1	0.1	0.1	0.1	<0.001
Tozeuma carolinense	1.1	0.7	1.0	0.5	4.0	0.8	0.7	0.3	2.7	0.7	3.5	1.3	0.001
Crab biomass	2.0	0.9	1.2	0.5	3.3	0.7	0.6	0.2	2.2	1.4	2.3	1.0	0.001
Shrimp biomass	0.9	0.4	1.7	0.9	4.1	0.7	1.5	0.3	2.6	0.6	3.1	0.5	<0.001
Total number of species	3.5	0.5	3.5	0.3	8.5	0.7	5.1	0.5	5.8	0.6	6.9	0.5	<0.001
Fall													
Fishes	5.5	3.4	5.6	2.8	6.2	1.3	5.1	0.6	8.8	1.4	6.1	0.6	<0.001
Anchoa mitchilli	5.5	3.4	4.9	2.6	1.4	1.1	0.0	0.0	0.0	0.0	0.1	0.1	0.008
Gobiosoma robustum	0.0	0.0	0.0	0.0	1.8	0.3	3.4	0.5	5.3	1.2	3.8	0.6	<0.001
Lagodon rhomboides	0.0	0.0	0.0	0.0	0.8	0.2	0.6	0.2	2.3	0.5	1.5	0.5	<0.001
Fish biomass	0.5	0.3	1.2	0.6	11.9	3.0	2.7	0.8	8.1	1.8	5.3	1.4	<0.001
Decapods	3.4	0.8	3.9	0.8	60.8	11.3	45.0	6.5	40.8	6.7	53.3	7.6	<0.001
Alpheus heterochaelis	0.0	0.0	0.0	0.0	5.3	1.9	1.1	0.4	2.1	0.6	7.2	1.5	<0.001
Dyspanopeus texana	0.0	0.0	0.0	0.0	16.7	4.7	9.9	3.4	14.3	2.8	20.8	4.7	<0.001
Callinectes sapidus	0.0	0.0	0.1	0.1	0.9	0.3	0.8	0.3	0.3	0.1	0.1	0.1	<0.001
Farfantepenaeus aztecus	0.1	0.1	0.3	0.1	1.5	0.4	0.5	0.2	0.6	0.2	0.3	0.1	<0.001
Farfantepenaeus duorarum	0.1	0.1	0.0	0.0	4.3	0.9	4.2	0.9	4.1	0.7	2.6	0.4	<0.001
Hippolyte zostericola	0.0	0.0	0.0	0.0	23.5	5.8	13.3	2.3	14.0	2.7	17.5	3.0	<0.001
Pagurus criniticornis	2.3	0.7	2.3	0.5	1.3	0.5	0.5	0.2	0.8	0.3	0.8	0.3	0.003
Tozeuma carolinense	0.0	0.0	0.0	0.0	3.5	0.9	14.1	3.7	1.9	0.8	1.5	0.9	<0.001
Crab biomass	0.1	0.1	0.1	0.1	4.5	2.1	2.8	1.0	6.8	3.7	4.7	1.2	<0.001
Shrimp biomass	0.0	0.0	0.0	0.0	4.2	1.0	2.1	0.4	3.1	0.6	4.6	0.8	<0.001
Total number of species	1.7	0.3	2.3	0.4	9.5	0.7	7.1	0.4	8.0	0.6	7.9	0.5	<0.001

was the only dominant species to exhibit seasonally different habitat use patterns: densities in *Halodule* during spring were the lowest of any seagrass, while densities were the highest in *Halodule* during fall (Fig. 5). Annual variations in *Tozeuma carolinense* abundance were not apparent except at the nonvegetated dredged material sites, where spring densities were higher in 1997 than in 1996.

*Alpheus heterochaelis* was also among the more abundant shrimps. This species, which makes deep permanent burrows, appeared to be most numerous each year and each season in revegetated dredged deposits and in *Thalassia* (Fig. 6), although variation between years was apparent. Densities were probably underestimated due to their burrowing habits.

Two swimming crabs, *Callinectes similis* and the commercially valuable *C. sapidus*, were occasionally abundant (Fig. 6). *Callinectes similis* appeared to select revegetated dredged deposits and *Halodule* beds in the spring, but densities were much lower ( $< 1$  ind  $m^{-2}$ ) during fall. *Callinectes sapidus* demonstrated an opposing seasonal trend, exhibiting low densities during spring and using old and new dredged material deposits during fall.



Table 3. Summary of a priori contrasts testing for significant differences in mean densities between: a) new dredged material (ND) and all vegetated habitat types (VG); b) revegetated dredged material (RE) and natural seagrass (SG); and c) natural seagrasses (HA = *Halodule*, SY = *Syringodium*, TH = *Thalassia*). Habitat type with higher mean density is listed for contrasts with  $P < 0.01$ .

Parameter	ND vs VG	P	RE vs SG	P	HA vs SY	P	HA vs TH	P	SY vs TH	P
<b>Spring</b>										
Fishes	VG	<0.001		0.472		0.186	TH	<0.001	TH	0.002
<i>Gobiosoma robustum</i>	VG	0.002		0.123		0.351	TH	0.001	TH	0.009
<i>Lagodon rhomboides</i>	VG	<0.001		0.044		0.407	TH	<0.001	TH	0.005
Fish biomass	VG	<0.001		0.169		0.675	TH	0.002	TH	0.008
Decapods	VG	<0.001		0.017		0.613		0.100		0.253
<i>Alpheus heterochaelis</i>	VG	0.001		0.145		0.326	TH	<0.001	TH	<0.001
<i>Callinectes similis</i>		0.025	RE	<0.001	HA	<0.001	HA	<0.001		0.389
<i>Dyspanopeus texana</i>	VG	<0.001	RE	<0.001		0.068	TH	0.001		0.153
<i>Farfantepenaeus aztecus</i>	VG	<0.001		0.393		0.391	HA	<0.001	SY	0.001
<i>Farfantepenaeus duorarum</i>	VG	<0.001		0.031		0.671		0.184		0.364
<i>Hippolyte zostericola</i>	VG	<0.001		0.360		0.502	TH	<0.001	TH	0.002
<i>Pagurus criniticornis</i>	ND	0.005	RE	0.005		0.795		0.870		0.924
<i>Tozeuma carolinense</i>	VG	0.003		0.013		0.021		0.058		0.674
Crab biomass		0.180	RE	<0.001		0.222		0.059		0.499
Shrimp biomass	VG	<0.001	RE	0.017		0.233		0.026		0.291
Total number of species	VG	<0.001	RE	0.001		0.423		0.012		0.083
<b>Fall</b>										
Fishes	VG	<0.001		0.391		0.114		0.476		0.383
<i>Anchoa mitchilli</i>	ND	<0.001		0.157		1.000		0.797		0.797
<i>Gobiosoma robustum</i>	VG	<0.001	SG	<0.001		0.124		0.761		0.217
<i>Lagodon rhomboides</i>	VG	<0.001		0.227	SY	<0.001		0.085		0.064
Fish biomass	VG	<0.001		0.059	SY	0.005		0.133		0.199
Decapods	VG	<0.001		0.676		0.484		0.476		0.159
<i>Alpheus heterochaelis</i>	VG	<0.001		0.652		0.177	TH	<0.001	TH	<0.001
<i>Callinectes sapidus</i>	VG	0.001	RE	0.008		0.134	HA	0.006		0.217
<i>Dyspanopeus texana</i>	VG	<0.001		0.508		0.065	TH	0.002		0.191
<i>Farfantepenaeus aztecus</i>	VG	0.001	RE	<0.001		0.586		0.397		0.165
<i>Farfantepenaeus duorarum</i>	VG	<0.001		0.924		0.934		0.146		0.125
<i>Hippolyte zostericola</i>	VG	<0.001		0.820		0.864		0.339		0.261
<i>Pagurus criniticornis</i>	ND	<0.001		0.294		0.359		0.418		0.913
<i>Tozeuma carolinense</i>	VG	<0.001		0.784	HA	<0.001	HA	<0.001		0.337
Crab biomass	VG	<0.001		0.782		0.115		0.017		0.410
Shrimp biomass	VG	<0.001		0.923		0.254	TH	0.004		0.081
Total number of species	VG	<0.001		0.073		0.521		0.427		0.878

The final two nekton dominants were also crabs. Densities of *Pagurus criniticornis* were generally similar among habitat types and seasons with the exception of spring 1996 (Fig. 7), when mean densities in the newly planted dredged material were exceptionally high. This was due to two samples from the south experimental site that yielded 107 of the 179 total *Pagurus criniticornis* collected during the entire study. Densities of *Dyspanopeus texana* were significantly higher in revegetated dredged deposits than elsewhere during spring, but there were no differences among the four seagrass habitat types during fall (Fig. 7). The only evidence of interannual variation in density of *Dyspanopeus texana* was found during the fall in *Thalassia*, when densities were higher in 1997.

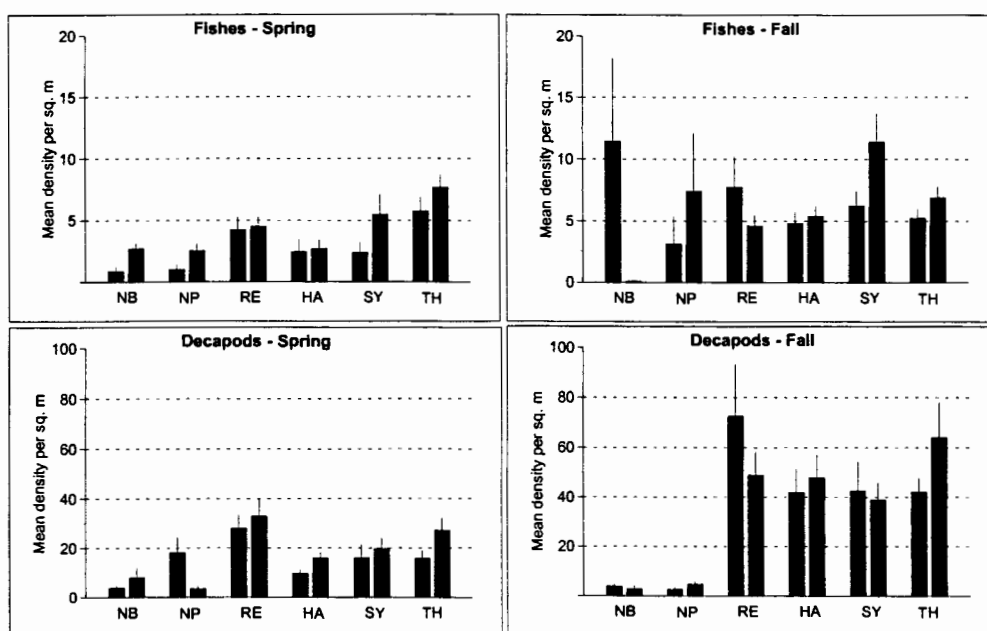


Figure 2. Seasonal densities (mean + SE) of total fishes and decapods in dredged material deposits (NB = new, bare; NP = new, planted; RE = revegetated) and in natural seagrass beds (HA = *Halodule*; SY = *Syringodium*; TH = *Thalassia*). In each pair of bars, left = 1996 and right = 1997.

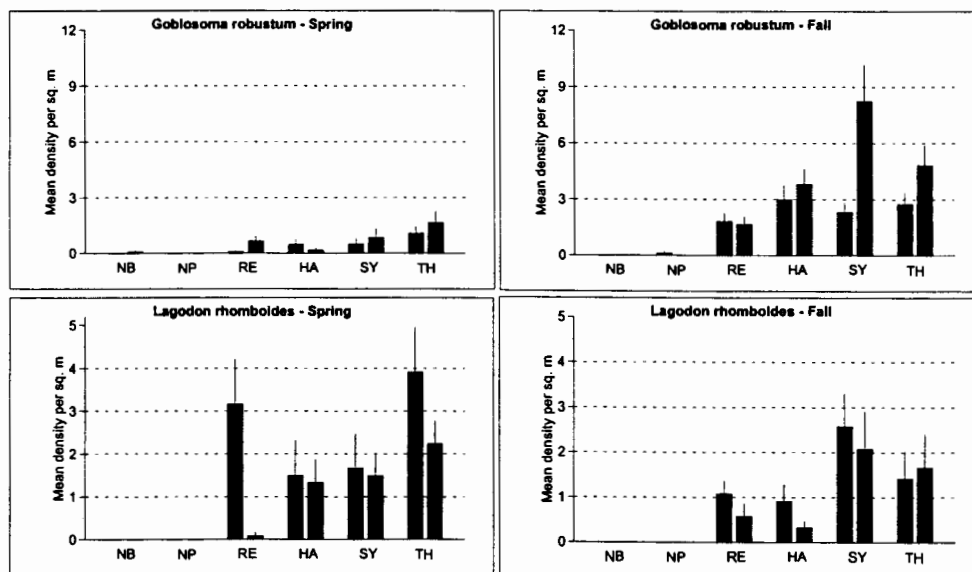


Figure 3. Seasonal densities (mean + SE) of dominant fishes in dredged material deposits (NB = new, bare; NP = new, planted; RE = revegetated) and in natural seagrass beds (HA = *Halodule*; SY = *Syringodium*; TH = *Thalassia*). In each pair of bars, left = 1996 and right = 1997.

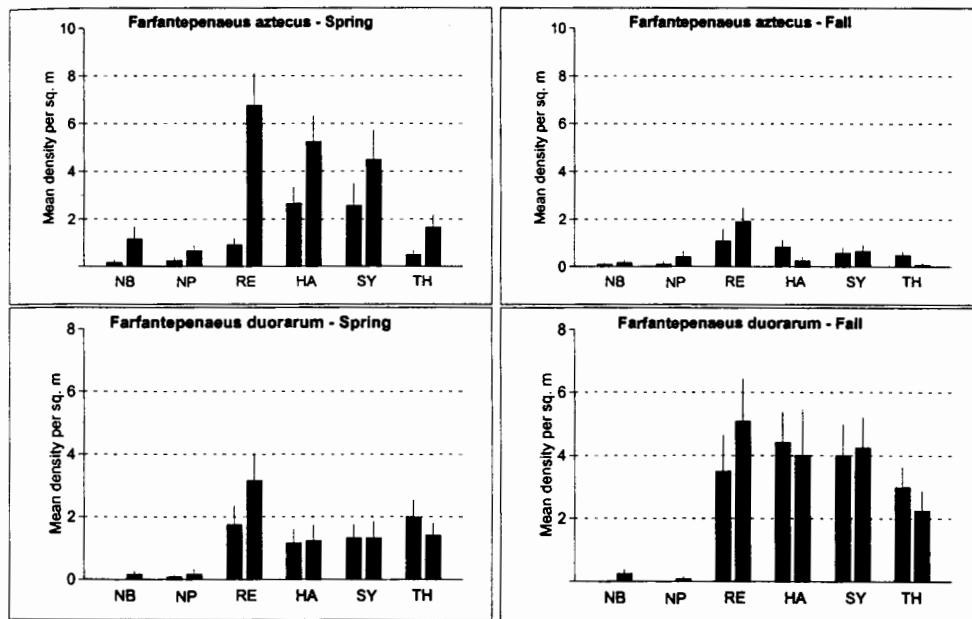


Figure 4. Seasonal densities (mean + SE) of commercial shrimps in dredged material deposits (NB = new, bare; NP = new, planted; RE = revegetated) and in natural seagrass beds (HA = *Halodule*; SY = *Syringodium*; TH = *Thalassia*). In each pair of bars, left = 1996 and right = 1997.

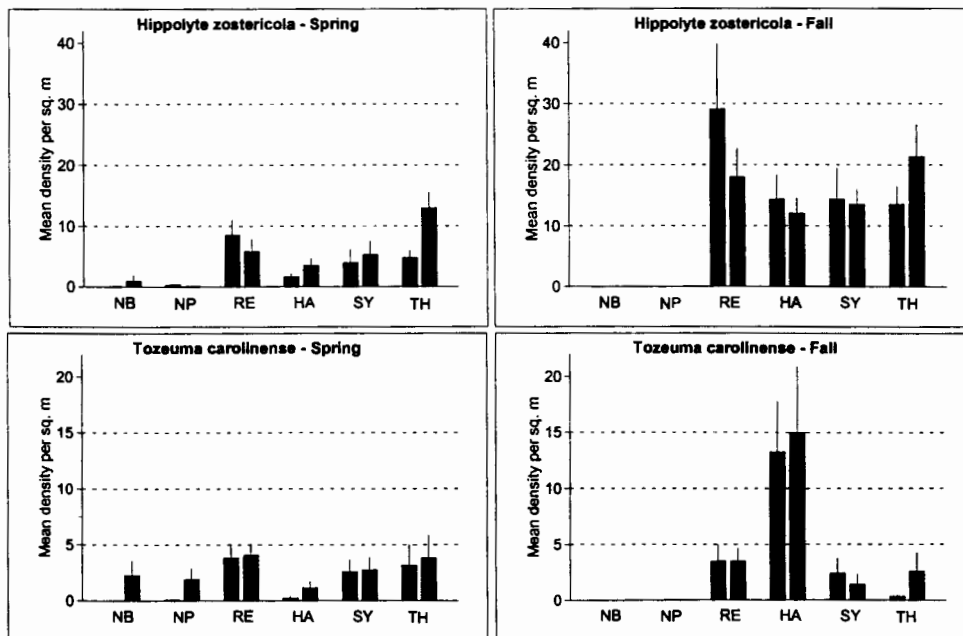


Figure 5. Seasonal densities (mean + se) of seagrass canopy shrimps in dredged material deposits (NB = new, bare; NP = new, planted; RE = revegetated) and in natural seagrass beds (HA = *Halodule*; SY = *Syringodium*; TH = *Thalassia*). In each pair of bars, left = 1996 and right = 1997.

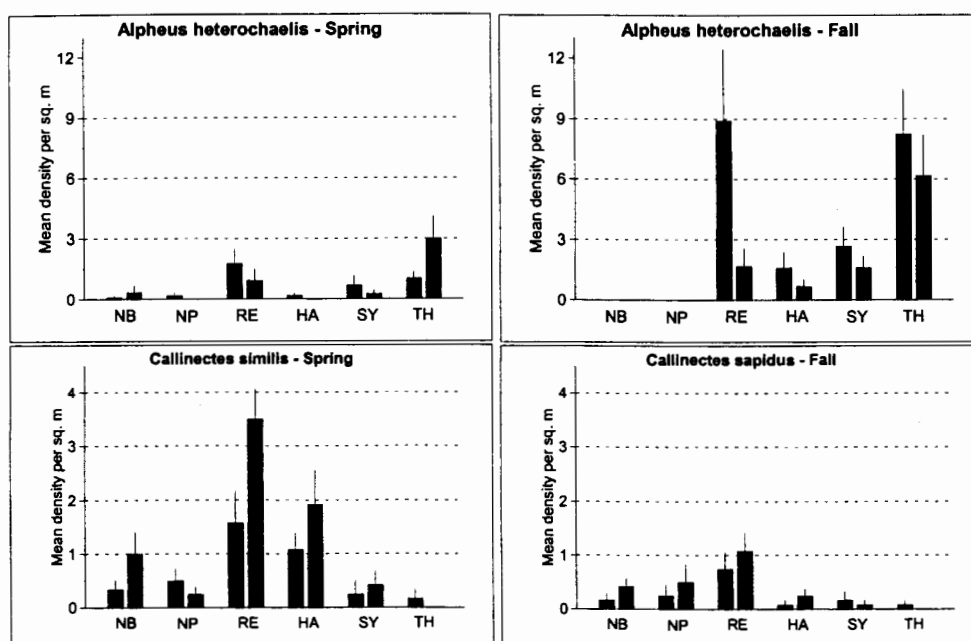


Figure 6. Seasonal densities (mean + SE) of a burrowing shrimp and two swimming crabs in dredged material deposits (NB = new, bare; NP = new, planted; RE = revegetated) and in natural seagrass beds (HA = *Halodule*; SY = *Syringodium*; TH = *Thalassia*). In each pair of bars, left = 1996 and right = 1997. Note change in crab species with season.

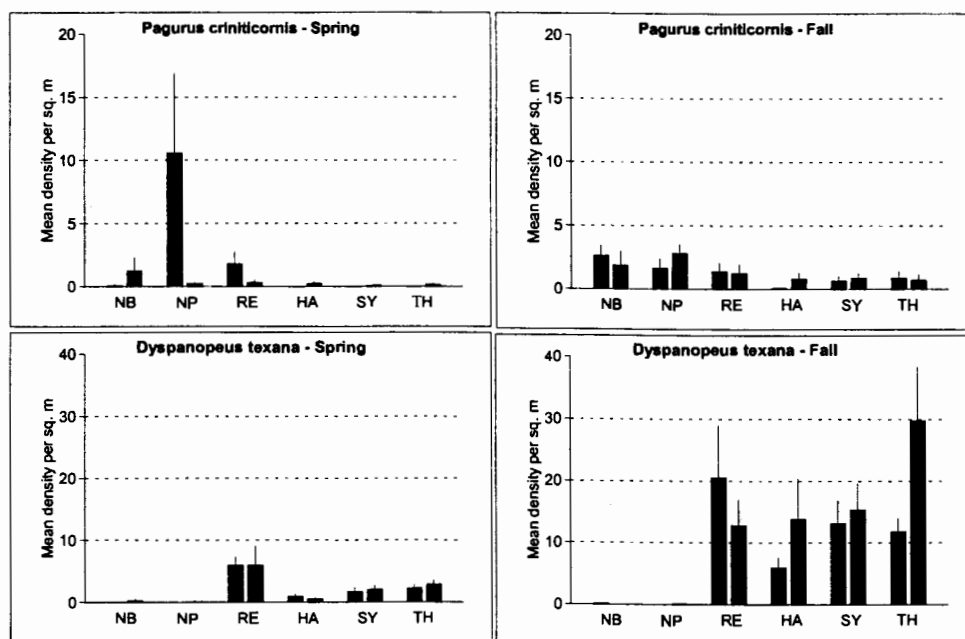


Figure 7. Seasonal densities (mean + SE) of epibenthic crabs in dredged material deposits (NB = new, bare; NP = new, planted; RE = revegetated) and in natural seagrass beds (HA = *Halodule*; SY = *Syringodium*; TH = *Thalassia*). In each pair of bars, left = 1996 and right = 1997.

Table 4. Habitat characteristics (mean and standard error, SE) of three types each of dredged material deposits and natural seagrass beds in Lower Laguna Madre, Texas, during spring (April 1996 and 1997) and fall (October 1996 and September 1997) seasons. P values for the ANOVA main effect of Habitat are given.

Parameter	Season	New, bare		New, planted		Revegetated		Halodule		Syringodium		Thalassia		P
		Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	
Seagrass														
Total seagrass shoots m <sup>-2</sup>	Spring	0	0	0	0	1,026	150	1,922	319	1,554	190	1,062	126	<0.001
	Fall	0	0	0	0	2,799	455	5,113	422	3,176	368	1,361	88	<0.001
Halodule shoots m <sup>-2</sup>	Spring	0	0	0	0	291	146	1,735	299	106	79	34	18	<0.001
	Fall	0	0	0	0	1,370	365	4,792	461	77	35	6	4	<0.001
Syringodium shoots m <sup>-2</sup>	Spring	0	0	0	0	468	142	133	66	1,337	205	160	82	<0.001
	Fall	0	0	0	0	780	199	198	72	2,927	390	47	27	<0.001
Thalassia shoots m <sup>-2</sup>	Spring	0	0	0	0	182	68	17	14	112	54	866	112	<0.001
	Fall	0	0	0	0	495	153	1	1	172	74	1,308	101	<0.001
Halophila shoots m <sup>-1</sup>	Spring	0	0	0	0	84	26	37	23	0	0	2	2	<0.001
	Fall	0	0	0	0	155	79	123	99	0	0	0	0	0.013
Seagrass shoot biomass (dry g m <sup>-2</sup> )	Spring	0.0	0.0	0.0	0.0	30.3	5.4	13.6	2.2	35.4	2.9	83.1	8.5	<0.001
	Fall	0.0	0.0	0.0	0.0	92.0	13.1	65.8	7.3	79.5	8.5	113.1	8.6	<0.001
Sediment														
NH <sub>4</sub> <sup>+</sup> content (μM)	Spring	322.7	67.4	281.7	62.5	41.2	6.9	33.2	4.8	37.3	5.2	26.4	4.8	<0.001
	Fall	190.0	40.7	173.8	32.3	32.9	3.3	35.0	4.8	35.4	4.8	21.8	2.2	<0.001
Organic content (%)	Sp 1996	1.7	0.2	1.8	0.1	2.1	0.3	3.3	0.2	3.5	0.3	3.3	0.3	<0.001
	Fa 1997	3.0	0.4	2.7	0.4	2.6	0.2	3.4	1.8	4.9	3.3	6.1	0.4	<0.001
Sand content (%)	Sp 1996	41.4	6.7	53.3	4.0	80.5	3.9	71.9	2.2	64.2	5.4	72.8	2.7	<0.001
	Fa 1997	61.4	5.5	58.0	5.3	67.5	5.0	59.0	2.2	56.7	3.1	56.9	4.8	0.469
Water column														
Depth (cm)	Spring	116	2.8	104	2.6	82	1.5	119	2.8	115	2.3	116	2.2	<0.001
	Fall	118	3.2	112	2.3	94	2.4	118	3.1	118	3.5	118	2.7	<0.001
Salinity (psu)	Spring	29	1.1	29	0.8	28	1.2	29	1.2	29	0.9	29	0.8	0.982
	Fall	33	0.5	30	0.4	33	0.4	31	0.9	32	0.7	32	0.9	0.023
Temperature (°C)	Spring	23.1	0.4	23.6	0.5	23.2	0.4	24.0	0.5	23.8	0.4	23.7	0.5	0.680
	Fall	26.7	0.2	26.6	0.2	26.9	0.5	26.8	0.3	27.0	0.4	26.7	0.3	0.987
Turbidity (ntu)	Spring	54	9.2	54	9.7	60	8.8	11	2.0	9	1.4	10	1.9	<0.001
	Fall	8	1.2	4	0.7	5	0.7	3	0.6	2	0.3	2	0.2	<0.001
Oxygen (ppm)	Spring	7.7	0.4	7.7	0.4	7.6	0.3	7.8	0.2	7.4	0.2	7.5	0.3	0.462
	Fall	6.4	0.1	7.4	0.1	8.0	0.5	6.6	0.3	6.8	0.3	6.6	0.2	0.002

SEAGRASS, SEDIMENT, AND WATER COLUMN CHARACTERISTICS.—Quantitative and qualitative measurements of seagrass coverage at the north and south experimental sites indicated that no seagrasses survived from two 1995 planting efforts and that none naturally colonized the experimental dredged material deposits during our study period (Table 4). No transplants were ever found in drop traps or throw traps deployed on the deposits during 1996 and 1997, and no live seagrass was noted by snorkeling over the sites.

Old, naturally revegetated deposits north and south of the experimental sites supported mixtures of *Halodule*, *Halophila*, *Syringodium*, and *Thalassia* with total shoot densities and aboveground biomasses similar to those found in one or more of the undisturbed seagrass habitat types to the east and west (Tables 4,5). Coverage in each of the three natural seagrass beds was dominated by one species (usually 85% of the total shoots m<sup>-2</sup>) but also supported an understory of one to three other species. *Halodule* beds often had up to three other species of seagrasses mixed in, but *Syringodium* and *Thalassia* usually only had each other for understory species. *Halophila engelmannii* was only found where *Halodule* was present. Total shoot densities in *Halodule* beds were usually significantly higher than those in *Thalassia* beds, while *Syringodium* shoot

Table 5. Summary of a priori contrasts testing for significant differences in mean habitat characteristics between: a) new dredged material (ND) and all vegetated habitats (VG); b) revegetated dredged material (RE) and natural seagrass (SG); and c) pairs of natural seagrasses (HA = *Halodule*, SY = *Syringodium*, TH = *Thalassia*). Only comparisons with significant differences are listed. Habitat type with higher mean density is listed for contrasts with  $P < 0.01$ .

Parameter	ND vs VG	P	RE vs SG	P	HA vs SY	P	HA vs TH	P	SY vs TH	P
<b>Spring</b>										
Seagrass										
shoot density	VG	<0.001	SG	0.009		0.787		0.042		0.077
shoot biomass	VG	<0.001	SG	0.010	SY	<0.001	TH	<0.001	TH	<0.001
<b>Sediment</b>										
organic content	VG	<0.001	SG	<0.001		0.567		0.893		0.683
sand content	VG	<0.001		0.048		0.285		0.881		0.224
<b>Water</b>										
depth		0.188	SG	<0.001		0.356		0.572		0.719
turbidity	ND	<0.001	RE	<0.001		0.571		0.856		0.701
<b>Fall</b>										
Seagrass										
shoot density	VG	<0.001		0.371	HA	<0.001	HA	<0.001	SY	<0.001
shoot biomass	VG	<0.001		0.749		0.312	TH	<0.001	TH	0.005
<b>Sediment</b>										
NH <sub>4</sub> <sup>+</sup> content	ND	<0.001		0.369		0.857		0.024		0.032
organic content	VG	<0.001	SG	<0.001	SY	0.005	TH	<0.001		0.038
<b>Water</b>										
depth		0.163	SG	<0.001		0.924		0.883		0.958
salinity		0.675	SG	0.025		0.128		0.430		0.461
turbidity	ND	<0.001	RE	<0.001		0.636		0.914		0.562
oxygen		0.825	RE	<0.001		0.709		0.975		0.686

Table 6. Linear regression models relating log-transformed densities of major nekton taxa to habitat variables: four seagrass species including *Halodule wrightii* (HA), *Halophila engelmannii* (HE), *Syringodium filiforme* (SY), and *Thalassia testudinum* (TH), coupled to measures of their abundance, including shoot density (Den), shoot biomass (Wgt), and % cover (Cov); sediment  $\text{NH}_4^+$  ( $\text{NH}_4$ ), % organic content (Org), and % sand content (Sand); and water temperature (Temp), salinity (Sal), depth (Dep), turbidity (Turb), and dissolved oxygen (Oxy). Variables are listed by sign and order of inclusion by forward stepwise regression.

Taxon	Season	Regression					Initial		P
		Step 1	Step 2	Step 3	Step 4	Step 5	r <sup>2</sup>	F	
Fishes	Spring	+THCov	+HECov				0.436	0.476	27.785
	Fall	-NH <sub>4</sub>	+SYDen				0.408	0.502	31.182
<i>Gobiosoma robustum</i>	Spring	+Org	+THWgt	-SYDen			0.305	0.501	22.108
	Fall	+SYDen	-Sal	+Temp	+THDen	+HACov	0.323	0.644	19.094
<i>Lagodon rhomboides</i>	Spring	+THCov	+SYCov				0.582	0.605	46.218
	Fall	+SYWgt	+THWgt				0.247	0.432	23.817
Decapods	Spring	-Dep	+THWgt	+SYCov			0.241	0.467	18.248
	Fall	+Temp	+HADen	+THWgt	+SYCov	+HEWgt	0.471	0.787	45.089
<i>Alpheus heterochaelis</i>	Spring	+THCov	+Oxy	-Temp			0.223	0.347	11.449
	Fall	+THWgt	+Temp	-Sand	-HEWgt		0.292	0.488	15.308
<i>Dyspanopeus texana</i>	Spring	+THCov	+SYDen	+HECov			0.294	0.448	16.933
	Fall	+THWgt	+Temp	+SYCov	+HADen		0.354	0.694	34.867
<i>Farfantepenaeus aztecus</i>	Spring	+HACov	+Org				0.163	0.271	11.967
	Fall	+Oxy	+HEDen				0.248	0.418	22.533
<i>Farfantepenaeus duorarum</i>	Spring	+THCov	+SYCOV	+HEDen	+HACov	-Dep	0.250	0.462	11.132
	Fall	+Temp	-NH <sub>4</sub>	+Sal			0.326	0.444	16.974
<i>Hippolyte zostericola</i>	Spring	+THCov	+SYCov	-Dep	-Turb		0.389	0.657	29.287
	Fall	+Temp	+THDen	+HAWgt	+SYWgt		0.442	0.756	47.529
<i>Pagurus criniticornis</i>	Spring	-Dep	+NH <sub>4</sub>	+Oxy	+Temp		0.143	0.319	7.921
	Fall	+Sal					0.065	0.065	5.189
<i>Tozeuma carolinense</i>	Spring	+THWgt	+SYCov	-Temp	-Dep	+Oxy	0.284	0.707	29.427
	Fall	+HADen	+Oxy	+Org			0.444	0.540	24.496



densities were intermediate (Tables 4,5). Shoot biomass was always highest in *Thalassia* and lowest in *Halodule*, and there were often significant differences in shoot biomass among habitat types.

There were several differences in substrate variables among habitat types. The newly deposited dredged material compacted to some degree over time, but most likely the fine components were re-suspended and transported away by currents as observed at nearby open bay placement sites (Brown and Kraus, 1996). This loss of fines was reflected in the increased percentages of sand and decreased percentages of silt and clay at the experimental sites between spring 1996 and fall 1997 (Table 4). By the latter period, there were no significant differences among the six habitats in sediment sand content (Table 5). Organic matter contents of new and old dredged material deposits were significantly lower than those found in natural seagrass. Significant differences in sediment organic matter were detected among natural seagrass beds, but only in the fall (Tables 4,5). Sediment  $\text{NH}_4^+$  concentrations were significantly higher in pore waters of new deposits at experimental sites than in other habitat types during all sampling periods (Tables 4,5), although levels decreased from  $>400 \mu\text{M}$  in April 1996 to  $<150 \mu\text{M}$  by September 1997. The south experimental site exhibited  $\text{NH}_4^+$  concentrations that were often 2 to 4 times higher than those observed at the north experimental site. The opposite trend was seen at the old revegetated deposits, although the  $\text{NH}_4^+$  concentrations were much lower. Significant differences in  $\text{NH}_4^+$  were detected among natural seagrass beds, but only in the fall.

Although there were no significant differences in water temperature among habitats within seasons, there were differences in other water column parameters (Tables 4,5). Water depth over the experimental deposits was observed to increase over time, from partially emergent in November 1994 to 112–120 cm depths by September 1997, similar to that found in the natural seagrass beds to the east and west. Water depths at the old revegetated placement areas were significantly shallower (by about 20 cm) than those observed elsewhere in both seasons. This was due to restricted sampling depths caused by steeply sloping sides at the south site and by lack of seagrass growth in deeper waters at the north site. Although significant differences in salinity and dissolved oxygen were occasionally observed among habitats (Tables 4,5), the magnitudes of difference were slight (e.g., 3 psu and 1.6 ppm) and were attributable to variations in rainfall, cloud cover, and diel dissolved oxygen patterns among sampling days. Turbidity values at new and old dredged material sites were significantly higher than those observed over natural seagrass beds (Tables 4,5), stemming from use of the open bay placement areas by dredgers at the same time this experiment started. Turbidity was higher in spring than in fall due to higher wind speeds in spring (Brown and Kraus, 1996).

**HABITAT RELATIONSHIPS.**—Regression models indicated that densities of total fishes, total decapods, and most dominant species could be related primarily to seagrass characteristics and secondarily to sediment or water column parameters (Table 6). However, the regression models for all taxa but one changed seasonally. *Lagodon rhomboides* densities were related to just two variables each season, both indicating abundance of *Thalassia* or *Syringodium*. The only species densities not related to seagrass parameters were those of *Pagurus criniticornis* (spring and fall) and *Farfantepenaeus duorarum* (fall). Although collected from all habitats, *P. criniticornis* was found at highest densities on the nonvegetated experimental sites. This was also the only species where sediment  $\text{NH}_4^+$  concentration was a positive factor in a regression model, and  $\text{NH}_4^+$  only entered the model in the spring when  $\text{NH}_4^+$  concentrations were highest. However, the regression

equations developed for *Pagurus criniticornis* were among the weakest of all species, so we do not have a good idea of the factors that might affect the abundance of this species. Seagrass parameters were almost always positive factors when included in the regression models (Table 6), with the only exceptions being in one model each for *Gobiosoma robustum* and *Alpheus heterochaelis*, both of which included positive and negative seagrass factors. In addition, *Thalassia* and *Syringodium* appeared together in 12 of 16 final regression models including either species, probably because these two seagrass species co-occurred in about half of all floral samples from *Thalassia*, *Syringodium*, and revegetated dredged material sampling sites. No other plant or environmental variables were consistently related to organism densities.

## DISCUSSION

This study provided quantitative estimates of fish and decapod densities for the southern half of Lower Laguna Madre. Faunal densities and biomass at the nonvegetated experimental sites were generally lower than those of seagrass habitats, less so for fishes than for decapods. Species compositions were also affected by lack of vegetation, in that water column fishes such as anchovies were more numerous in nonvegetated habitats and epibenthic fishes dominated seagrass habitats. Nonvegetated mud or sand habitats typically exhibit significantly lower faunal densities than do adjacent seagrasses (Summerson and Peterson, 1984; Fonseca et al., 1990; Sogard and Able, 1991; Humphries et al., 1992; Connolly, 1994; Sheridan et al., 1997; but see Sheridan, 1992 for exceptions). This pattern suggests seagrasses provide food or refuge for many fishes and invertebrates, and there are species that are adapted to life in vegetated habitats that are not found in bare mud or sand habitats (Sheridan, 1992). Once dredged material revegetates, it appears to support high densities and diversities of fishes and decapods typical of undisturbed seagrasses in Laguna Madre. The time required for these Laguna Madre deposits to revegetate and recover to similar faunal densities and diversities remains unknown. In the Indian River Lagoon of Florida, undisturbed seagrass beds and revegetated dredged deposits with similar macrofaunal densities exhibit differences in species composition and community indices even after 31 yrs (Brown-Peterson et al., 1993).

Overall abundance of decapods did not appear to be related to seagrass type, but seagrass type did appear to influence distributions of total fishes and of some species in Lower Laguna Madre. *Lagodon rhomboides*, for example, was most abundant in *Thalassia* or *Syringodium* beds and least abundant in *Halodule*. During spring, *Gobiosoma robustum* and the total fish fauna were most abundant in *Thalassia* beds. *Alpheus heterochaelis*, *Dyspanopeus texana*, and *Hippolyte zostericola* also were most abundant in *Thalassia*, while *Callinectes similis* (spring) and *Tozeuma carolinense* (fall) were most abundant in *Halodule* beds. *Farfantepenaeus aztecus* occurred mainly in spring and was abundant in both *Halodule* and *Syringodium* beds. In other studies (all conducted in Florida) that have examined densities of these nekton species, there seems to be little consistency as to which adjoining seagrass types harbor higher animal densities. Highest densities of *Lagodon rhomboides*, *Gobiosoma robustum*, and *Hippolyte zostericola* occur in *Thalassia* in Florida Bay (Sheridan et al., 1997) and Apalachee Bay (Lewis, 1984) but not in the Indian River Lagoon where densities are highest in *Halodule* or *Syringodium* (Stoner, 1983; Zupo and Nelson, 1999). Also in Indian River Lagoon, Brown-Peterson et al. (1993)

report higher densities of *Lagodon rhomboides* in *Halodule* than in mixed *Halodule-Syringodium* but the reverse for *Gobiosoma robustum*. In Florida Bay, densities of *Farfantepenaeus duorarum* are highest in *Halodule* (Sheridan et al., 1997) but we did not find higher densities associated with any seagrass type in Lower Laguna Madre. In contrast, *Alpheus heterochaelis* densities are highest in *Thalassia* both in Lower Laguna Madre and Florida Bay (Sheridan et al., 1997). To our knowledge, there is no other comparative information for seagrass selection by other dominant species found in Lower Laguna Madre.

Enclosure samplers such as the drop trap used here are recommended for estimating densities of small fishes and decapods in shallow waters because they are quantitative and have high catch and recovery efficiencies that are similar among habitat types (Rozas and Minello, 1997). However, the small area of the drop trap adequately estimates densities only of relatively abundant species unless a large number of samples is available (see examples in Minello, 1999). We note that habitat-related differences in density may exist among less abundant, but nevertheless ecologically or economically important, species. For example, we captured too few specimens of predatory gamefishes such as spotted seatrout *Cynoscion nebulosus*, southern flounder *Paralichthys lethostigma*, and red drum *Sciaenops ocellatus* or the economically important white shrimp *Litopenaeus setiferus* to judge apparent habitat preferences.

We do not know when dredging last impacted the revegetated sites, but our study indicated that when these areas eventually become colonized by seagrasses they can become as productive as undisturbed seagrass beds. Revegetation is not guaranteed, however, and will only be successful if sediments are not subjected to rapid erosion and if water column, substrate, and light conditions are favorable. The old revegetated deposits that we examined appeared to be outside the influence of the erosional forces affecting the experimental sites. The experimental deposit sites were located in a reach of Lower Laguna Madre where there is a strong cross-channel flow southwest to northeast across the GIWW resulting from a circulation gyre (Militello and Kraus, 1994). Deposits of fine materials in this area were apparently subjected to strong erosion and transport processes. Bathymetric mapping of open bay deposits before and after dredging near our experimental sites indicate that deposits are flattened out by this circulation feature in as little as 13 months (Brown and Kraus, 1996). In addition, field observations indicated that the new deposits probably had not finished settling and compacting even during our final sampling period almost three years post-dredging.

Seagrass transplants into this unstable sediment would have had to grow rapidly to offset compaction and erosion. We assessed water column and sediment properties that controlled seagrass growth at the experimental sites and nearby seagrass beds. Water quality was generally adequate to support survival and growth of transplanted seagrasses. Temperature and salinity measurements indicated well-mixed waters throughout the sampling area. Turbidity was higher at the experimental sites than elsewhere, which led to increased light attenuation and thus decreased light transmittance to the bottom. The underwater light regime at the experimental transplant sites was 15–20% of surface irradiance (SI) during the summer, less than half of that observed in control seagrass beds (K. Dunton, University of Texas, Port Aransas, TX, personal communication). These values exceeded the 14% SI minimum light requirements for *Thalassia* (Lee and Dunton, 1997) but were at the 18–25% SI minimum required for *Halodule* (Dunton, 1994; Dunton and Tomasko, 1994). In addition, sediment  $\text{NH}_4^+$  concentrations were much higher at experi-

mental sites than in seagrass beds and could have been a chronic stress on transplants. The combined effects of substrate instability and loss, elevated sediment  $\text{NH}_4^+$  concentrations, and chronic low light probably led to transplant loss.

The failure of all transplants prevented projection of revegetation rates in this study. Natural revegetation of dredged material deposits in Upper Laguna Madre is considered slow. Rickner (1979) found that seagrass remains relatively sparse at sites < 10 yrs old and approaches natural conditions only after > 20 yrs. However, recent observations at placement areas north of the experimental sites in both Lower Laguna Madre and Upper Laguna Madre indicate unassisted *Halodule*, *Halophila*, and *Ruppia* colonization and dense above-ground biomass within 3 yrs is possible at physically stable sites (Sheridan, 1999a).

Spring and fall densities of fishes and decapods in seagrass habitats examined in this study were generally lower than those in seagrass beds sampled with quantitative gear elsewhere in the Gulf of Mexico. Fish densities ranged from 3–9  $\text{m}^{-2}$  in seagrasses during our study of the southern reach of Laguna Madre. Proceeding north in Texas, ranges of fish densities in seagrass habitats are 8–17  $\text{m}^{-2}$  in middle reaches of Laguna Madre (Sheridan, 1999a), 8–14  $\text{m}^{-2}$  in northern Laguna Madre and Corpus Christi Bay (Sheridan, 1999b), 9–10  $\text{m}^{-2}$  in Mesquite Bay (Rozas and Minello, 1998), and 8–98  $\text{m}^{-2}$  in Christmas Bay (Sheridan et al., 2003). In Florida, ranges in fish densities are 5–13  $\text{m}^{-2}$  in Rookery Bay (Sheridan, 1992) and 7–75  $\text{m}^{-2}$  in Florida Bay (Sogard et al., 1987; Sheridan et al., 1997). Similar trends were noted for decapods, which in this study ranged from 13–61  $\text{m}^{-2}$  in southern Laguna Madre. The ranges of decapod densities in seagrass habitats are 20–90  $\text{m}^{-2}$  in Lower and Upper Laguna Madre north of the present study area (Sheridan, 1999a), 24–133  $\text{m}^{-2}$  in northern Laguna Madre and Corpus Christi Bay (Sheridan, 1999b), and 40–120  $\text{m}^{-2}$  in Christmas Bay (Sheridan et al., 2003). In Florida, decapod densities are 28–145  $\text{m}^{-2}$  in Rookery Bay (Sheridan, 1992) and 24–885  $\text{m}^{-2}$  in Florida Bay (Holmquist et al., 1989a,b; Sheridan et al., 1997).

Even though we found relatively low fish and decapod densities, fisheries productivity of Lower Laguna Madre is high. The lower standing crops of both fishes and decapods in our study area may be due to high densities of predators indicated from fishery landings data. Texas Parks and Wildlife Department monitors fishing in nine bay systems and four offshore areas along the Texas coast. Inshore finfish production within Lower Laguna Madre is second only to Upper Laguna Madre, while offshore finfish landings in southern Texas rank second behind the northern Texas coast (Robinson et al., 1997). Party boat fishing pressure and landings in Lower Laguna Madre are the highest of any Texas bay system (Campbell et al., 1991). Offshore shrimp landings often rank second behind the north-central Texas coast (Nance, 1993). The mechanism for maintaining system productivity likely resides in the 480  $\text{km}^2$  of seagrasses in Lower Laguna Madre (Quammen and Onuf, 1993), the third largest expanse of seagrasses in the northern Gulf of Mexico behind the Florida Bay–Florida Keys complex and the Florida Big Bend region (6475  $\text{km}^2$  and 3350  $\text{km}^2$ , respectively; Sargent et al., 1995). Although nekton standing crops are low, the vegetated area is large and apparently can sustain high secondary production.

Seagrasses can provide refuge and food for juvenile fishery and forage organisms (Heck et al., 1997). This study provided quantitative estimates of fish and decapod densities for the southern half of Lower Laguna Madre and indicated that revegetated dredged material can be as productive as adjacent natural seagrasses. Depositing dredged material in nonvegetated locations where erosional forces are minimized should lead to shallow

seagrass-covered banks. Alternatively, dredged material could be removed from the system permanently through offshore or upland disposal. Methods for conserving present seagrass habitats and enhancing recovery of seagrasses on dredged material placement areas, while keeping commercial waterways open, still need to be included in dredged material management plans.

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Appendix 1. Total number fishes and decapods collected from dredged material deposits [New, Bare (NB), New, Planted (NP), and Revegetated (RE)] and natural seagrass beds [*Halodule wrightii* (HA), *Syringodium filiforme* (SY), and *Thalassia testudinum* (TH)] in Lower Laguna Madre during 1996–1997. Biomass of total fishes and decapods, as well as total area sampled, are also listed.

Taxon	NB	NP	RE	HA	SY	TH
Fishes	169	159	253	184	306	307
<i>Anchoa hepsetus</i>	17	18	8	0	2	30
<i>Anchoa mitchilli</i>	132	114	43	1	2	4
<i>Archosargus probatocephalus</i>	0	0	1	0	0	1
<i>Bairdiella chrysura</i>	3	1	5	2	0	2
<i>Brevoortia patronus</i>	3	2	6	3	25	3
<i>Citharichthys spilopterus</i>	0	0	1	1	0	0
Clupeidae	3	1	3	2	0	5
<i>Cynoscion nebulosus</i>	0	0	2	0	0	0
<i>Etropus crossotus</i>	0	1	0	0	0	0
<i>Eucinostomus argenteus</i>	0	0	2	3	6	1
<i>Eucinostomus</i> sp.	0	0	0	0	1	0
Exocoetidae	0	0	2	1	0	0
<i>Gobiesox strumosus</i>	0	0	0	0	0	1
Gobiidae	0	0	0	1	4	0
<i>Gobionellus boleosoma</i>	0	1	11	1	4	0
<i>Gobiosoma bosc</i>	0	0	0	1	1	0
<i>Gobiosoma robustum</i>	1	1	51	90	143	124
<i>Harengula jaguana</i>	0	11	0	0	0	0
<i>Hippocampus zosterae</i>	1	0	6	2	7	5
<i>Lagodon rhomboides</i>	0	0	59	49	94	111
<i>Leiostomus xanthurus</i>	0	0	2	2	0	2
<i>Lucania parva</i>	0	0	0	0	1	0
<i>Menidia beryllina</i>	0	1	0	0	0	0
<i>Microgobius gulosus</i>	0	0	1	0	0	0
<i>Microgobius thalassinus</i>	0	0	3	0	0	0
<i>Micropogonias undulatus</i>	3	5	6	3	0	0
<i>Myrophis punctatus</i>	4	3	2	3	1	2
<i>Opsanus beta</i>	0	0	10	4	7	9
<i>Orthopristis chrysoptera</i>	0	0	3	1	1	1
<i>Paralichthys lethostigma</i>	1	0	0	0	0	0
Sciaenidae	0	0	1	0	0	1
<i>Sciaenops ocellatus</i>	0	0	3	0	0	0
<i>Symphurus plagiatus</i>	1	0	6	4	3	0
<i>Syngnathus louisianae</i>	0	0	1	0	0	0
<i>Syngnathus scovelli</i>	0	0	15	11	4	7
Unidentified larvae	0	0	2	0	0	0
Fish biomass (g wet)	31.28	45.13	620.48	96.71	227.64	228.51

## Appendix 1. Continued.

Taxon	NB	NP	RE	HA	SY	TH
Decapods	220	336	2,191	1,398	1,412	1,796
<i>Alpheus heterochaelis</i>	5	2	159	29	62	221
<i>Ambidexter symmetricus</i>	0	0	12	1	0	0
<i>Callinectes sapidus</i>	7	6	35	24	15	7
<i>Callinectes similis</i>	23	18	83	40	11	3
<i>Clibanarius vittatus</i>	1	0	8	0	1	2
<i>Dyspanopeus texana</i>	4	2	545	257	389	562
<i>Farfantepenaeus aztecus</i>	19	17	128	108	100	33
<i>Farfantepenaeus duorarum</i>	5	4	162	130	131	104
<i>Farfantepenaeus</i> spp.	0	1	21	31	17	3
<i>Hippolyte zostericola</i>	13	5	737	381	448	634
<i>Isocheles wurdemanni</i>	0	7	0	0	0	0
<i>Leptochela serratorbita</i>	0	2	0	0	0	0
<i>Libinia dubia</i>	0	1	8	3	5	11
<i>Litopenaeus setiferus</i>	0	0	3	4	4	2
<i>Pagurus annulipes</i>	0	0	0	0	2	0
<i>Pagurus criniticornis</i>	68	179	58	14	20	22
<i>Pagurus longicarpus</i>	36	56	2	4	6	4
<i>Pagurus pollicaris</i>	4	4	1	0	1	0
<i>Palaemonetes intermedius</i>	1	0	5	10	34	27
<i>Palaemonetes pugio</i>	1	0	4	0	1	4
<i>Palaemonetes vulgaris</i>	2	0	23	1	18	10
<i>Palaemonetes</i> sp.	1	0	0	1	4	4
<i>Panopeus herbstii</i>	0	0	13	0	26	19
<i>Panopeus turgidus</i>	0	0	6	2	6	3
<i>Petrolisthes armatus</i>	0	0	0	0	0	1
<i>Pinnixa lunzi</i>	0	0	0	2	1	1
<i>Rhithropanopeus harrisii</i>	1	0	3	0	0	0
<i>Rimapenaeus constrictus</i>	2	8	0	0	0	0
<i>Tozeuma carolinense</i>	27	24	179	356	110	119
Shrimp biomass (g wet)	21.85	40.76	198.99	85.99	137.21	183.33
Crab biomass (g wet)	50.22	29.49	187.81	81.25	217.07	168.85
Area sampled (m <sup>2</sup> )	47	45	48	48	48	48